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HABITAT STRUCTURE PROVIDED BY *MYTILUS EDULIS* AND THE MODIFICATION BY SESSILE INHABITANTS[1]

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To illustrate the habitat structure provided by a patch of the mussel *Mytilus edulis* L., we examined the size composition of the mussels, the change in shell morphology with growth, and the utilization patterns of the shells by sessile species. A *Mytilus* patch which developed on a rope suspended in the water for one year was examined. The spherical mass (diameter, about 20 cm) was composed of two groups of *Mytilus* having different sizes. A morphological difference between the larger (shell length $\geqq 4.0$ cm) and the smaller (shell length <4.0 cm) mussel groups indicated that the growth pattern of the shell changes with size in the patch: the growth along an antero-posterior axis was conspicuous in larger mussels. Since mussels faced their posterior ends to the outward portion of the patch, adhesive discs of neighboring mussels were concentrated on the anterior part of the shell showing that the inner part of the patch was characterized by a high density of byssal threads. Adhesive discs on the posterior part of the shell were less abundant on the larger mussels than on the smaller ones. This indicates that the peripheral part of the patch was constructed by the posterior part of larger mussels. Of nineteen sessile species found in the patch, ten occurred on the mussel shells. The shells of the larger mussels harbored almost all the sessile organisms (98% in wet weight; 94% in occurrence). A sponge *Halichondria* sp., the most abundant sessile species, preferably inhabited the surface of shells being attached by many adhesive discs which probably occupied the inner part of the patch. On the other hand, algae were attached to the posterior parts of large shells with only a few adhesive discs. In addition, overgrowth by sponges over other sessile species was frequent, indicating that the stucture of the *Mytilus* patch is determined by the habitation patterns of the sessile species on the mussel shells as well as by the mussel population structure.

INTRODUCTION

Habitat structure is worthy of greater attention as an ecological topic in its own right, rather than being treated simply as a routine component of all systems (McCOY *et al.*, 1991). In a marine system, macrobenthic organisms create or modify the physical structure of the microhabitat. The processes are categorized into three different types: habitat provision, habitat creation, and habitat conditioning (NISHIHIRA, 1992a, b, 1993). Of these processes, habitat provision refers to the process by which the body of an inhabitant provides secondary space for coloniza-

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tion by other species. For example, sessile organisms such as corals (ABELE, 1984), mussels (SUCHANEK, 1985; TSUCHIYA and NISHIHIRA, 1985, 1986; LOHSE, 1993), oysters (TSUCHIYA and HIRANO, 1985; MATSUMASA, 1994), macroalgae and seagrasses (NISHIHIRA, 1968; MUKAI, 1978, 1990; MATSUMASA and KURIHARA, 1988) provide distinct habitats for their associates such as sessile organisms and motile animals.

Mussels (family Mytilidae) have achieved a world-wide success as dominant space occupiers on rocky substrates in temperate marine habitats (SUCHANEK, 1985). A mussel *Mytilus californianus* Conrad is probably the most well-known representative in ecology as the best competitor for primary space (rock surface) in the exposed rocky mid-intertidal community of western North America (PAINE, 1966, 1974; DAYTON, 1971; HARGER, 1972). In Japan, another mussel *Mytilus edulis* L.[1] dominates exposed and semi-exposed rocky habitats (HOSHIAI, 1958, 1960, 1961; HOSOMI, 1967) in the same way as *M. californianus* in western North America. It is well-known that *M. californianus* has the potential capability to occupy all rock surfaces and to lower the diversity of competing species for primary space. However, LOHSE (1993) pointed out that the previous studies involving the relationship between *M. californianus* and the biodiversity did not consider an important fact that species which compete with *Mytilus* for primary space also use mussel shells as their substrates. In addition, almost all of the studies on 'community' found on hard substrates have not included many components (e.g., motile animals) of their communities (DEAN and CONNELL, 1987; UNDERWOOD and VERSTEGEN, 1988). Actually, beds and patches of *Mytilus* spp., as their structurally complex entities, provide diversified microhabitats for a variety of associated animals including small epi- and infaunal ones (SUCHANEK, 1979, 1980; TSUCHIYA, 1979; TSUCHIYA and NISHIHIRA, 1985, 1986). Therefore, it is important to clarify the roles of *Mytilus* spp. not only as dominant space occupiers, but also as habitat providers in structuring rocky shore communities.

As a habitat provider, a living individual of *Mytilus* offers three types of microhabitats for associates: the shell surface, the soft part, and the byssal threads. In addition, the inner space of dead mussel shells provides another type of microhabitat. On the other hand, a habitat structure provided by a gathering of *Mytilus* (e.g., space among mussel shells) may change due to the size/age composition of mussels and the spatial arrangement of each size/age group which is probably related to the patch size and age (TSUCHIYA and NISHIHIRA, 1985, 1986). In addition, a habitat provided by mussels is diversified further by inhabitations of other sessile species such as algae, sponges, and barnacles. Moreover, these sessile species may also provide microhabitats for other animals such as polychaetes and

1) Some authors refer to the mussel in Mutsu Bay as *Mytilus edulis galloprovincialis*. But, according to the previous studies done in the Asamushi area, this mussel is referred to as *M. edulis* in the present paper.

amphipods. This process is called a 'live-in system' by MUKAI (1978, 1990), and has been considered to be one of the three major mechanisms involved in promotion and maintenance of biodiversity (NISHIHIRA, 1992a, b, 1993). In order to test this hypothesis, we have recently started an experimental study on communities associated with *Mytilus edulis* patches developing on an artificial rope substrate.

It is important to clarify (1) the characteristics of habitat provided by *Mytilus* population, (2) patterns in diversifying microhabitats by sessile species, and (3) responses of colonizations by semi-sessile and motile animals. In order to examine points (1) and (2) which are concerned with microhabitat structuring agents, this study investigates a population structure of *Mytilus* and utilization patterns of *Mytilus* shells by other sessile species. For this, a spherical patch of *Mytilus* which developed on a rope submerged for 1 year was examined. For (3), the relationships between the microhabitat structuring agents and the other inhabitants (semi-sessile and motile fauna) will be discussed separately.

MATERIALS AND METHODS

A rope of seven meter length (diameter, 1.5 cm) with a buoy was anchored at a 6 meter depth near the Marine Biological Station, Tôhoku University (40°55′N: 140°50′E) on 14 July 1991. At a depth of 50 cm, the rope was knotted (overhand knot) to facilitate the development of the *Mytilus* patch. In the course of a year, a spherical mass of aggregation of *Mytilus* (diameter, about 20 cm) formed with the knot of the rope in the center. On 20 July 1992, the mussels with the associated organisms were peeled from the rope, collected into a plastic bag, and fixed with 10% buffered formalin.

In the laboratory, 'living mussels' with their soft parts and shells without soft parts (i.e., remains of dead mussels) were sorted. The mussels with shell length above 2.0 mm were dealt with in this study, although the newly-settled mussels are usually smaller (shell length, 0.8-1.5 mm; BAYNE, 1964; KAJIHARA *et al.*, 1978). Shell lengths, shell heights, shell widths, and lengths of anterior dorsal margin of shells (ADM) of 'living' mussels were measured using a pair of slide calipers. Simultaneously, a mussel was divided into two parts (i.e., posterior half and anterior one), and adhesive discs of byssal threads (including traces of discs) on shell surfaces were counted for each part. The number of adhesive discs on a posterior part of a mussel was used as an index for the location of the mussel in the patch. Areas of right shell profiles of mussels traced on graph paper ruled into 1 mm squares were measured and substituted for areas of shell surfaces. Sessile species observed on the shells were counted and peeled off. Then the weight of sessile species including shells or tubes was measured after being blotted with filter paper. The total weight of dead mussel shells was measured, and morphological characteristics of each shell were also measured if possible.

Mussels were divided into size groups according to the distribution of the shell length. For each size group, relationships between the shell length and the other characteristics of shell (height, width, and length of ADM) were analysed by a simple regression analysis (ordinary least squares). The differences between regression coefficients were examined by *t*-test. The mean number and the mean wet weights of sessile species observed on the *Mytilus* shell were compared for the size groups of *Mytilus*. In addition, the mussels were divided into two groups according to presence/absence of each sessile species. The shell length and the number of adhesive discs on shells were compared between these groups. The differences between sample means were examined by the Mann-Whitney U test.

RESULTS

There were few shells of dead mussels in the *Mytilus* patch. The total weight of dead mussel shells was 25.5 g. One pair of complete shells of a dead mussel was observed: the length and weight were 6.2 cm and 6.6 g, respectively. The shell length of living mussels displayed a bimodal distribution (Fig. 1). The maximum shell length observed was 7.2 cm. The mussels were roughly divided into two size groups: the mussels with shell length $\geq$4.0 cm ('large') and those with shell length $<$4.0 cm ('small'). We used mussels with shell width $\geq$0.2 cm for our analyses because of the difficulty in measurement of width below 0.2 cm. Thus the shell length of 'small' mussels used for analyses ranged from 0.7 cm to 4.0 cm. The relationships between the shell length and the shell height showed that the slope of regression line was significantly smaller (*t*-test, $p<0.05$; Fig. 2) in the large mussels than in the small ones. The relationships between the shell length and the length of ADM also showed that the slope of regression line was significantly smaller (*t*-test, $p<0.05$) in the large mussels than in the small ones. The ratios of the shell height to the length of ADM were not different for small and large mussels. Since this ratio is an approximation of the sine of the angle between the ventral margin and ADM of the shell, the result indicated that the angle was not different for the two size groups.

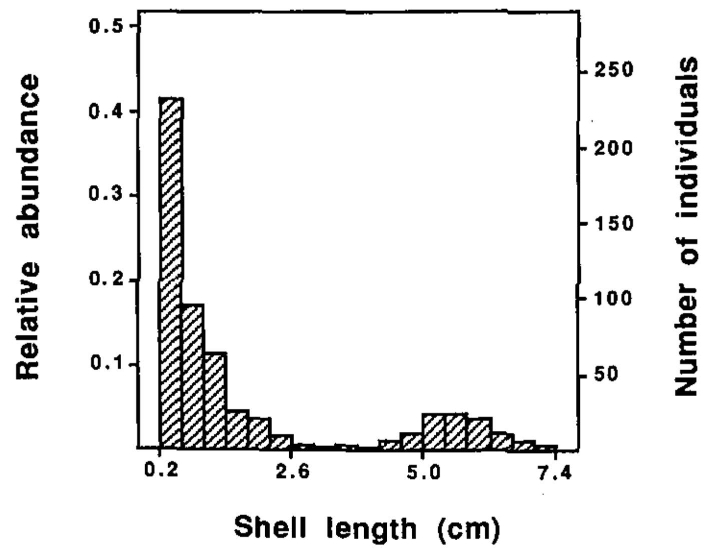

Fig. 1. Size distribution of *Mytilus edulis* forming a spherical patch on a rope suspended in the water for a year (from July 1991 to July 1992).

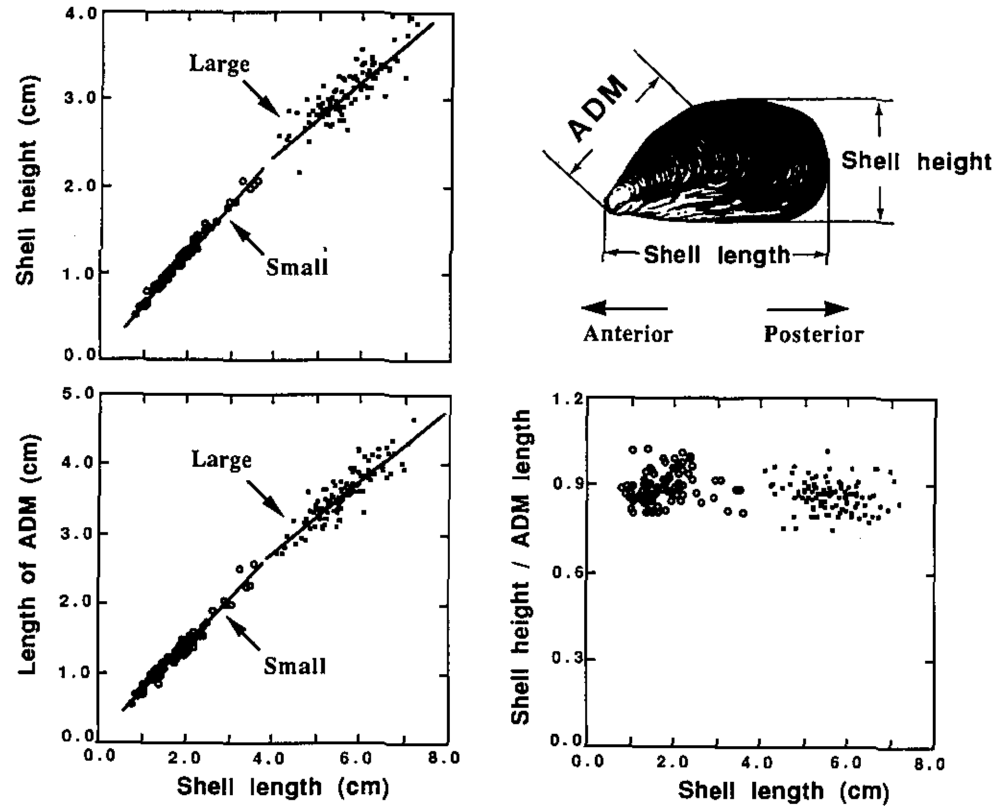

Fig. 2. Morphological characteristics of *Mytilus* shell. ADM, anterior dorsal margin of *Mytilus* shell. 'Large' is a group of mussels with their shell lengths of 4.0 cm over, and 'small' with their shell lengths from 0.7 cm to 4.0 cm (see text).

The number of adhesive discs on shells per mussel was significantly higher (U test, $p<0.001$) in the large mussels than in the small mussels (Fig. 3). On the other hand, the density of the adhesive discs was not significantly different for the two size groups (U test, $p>0.05$), but the density of the adhesive discs on the posterior parts of mussels was significantly lower in the large mussels than in the small ones (U test, $p<0.01$). These results indicate that the posterior part of the shell surface of the large mussel was used relatively less frequently for attachments by the byssal threads from neighbors than the small mussel. For the large and small mussels, 85

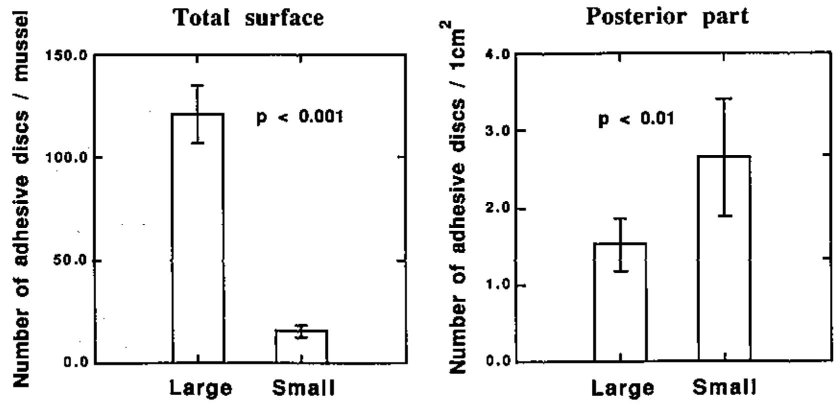

Fig. 3. Adhesive discs on mussel shells. Mean number for shells of a mussel (left) and mean density for a posterior part of shells of a mussel (right). Vertical bars show ± 1 SE. The 'large' and 'small' are the same groups of mussels as those in Fig. 2. The Mann-Whitney U test indicates the significant differences between means.

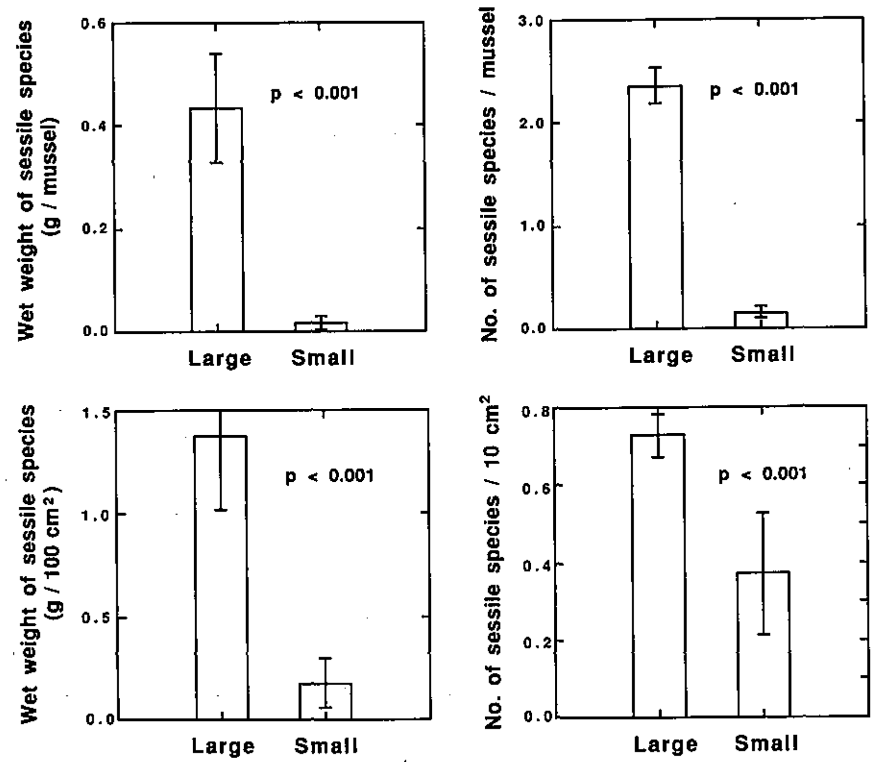

Fig. 4. Mean wet weight (left) and mean number (right) of sessile species observed on *Mytilus* shell surface. Vertical bars show ± 1 SE. The 'large' and 'small' are the same groups of mussels as those in Fig. 2. The Mann-Whitney U test indicates the significant differences between means.

and 80%, respectively, of the adhesive discs were observed on the anterior part of shells. The mean density of adhesive discs (number/1 cm²) on the anterior part was 3.8 times that on the posterior part for large mussels, and was 2.6 times that for small mussels.

The large mussels harbored more sessile species as indicated by the wet weight and the species richness than the small mussels (Fig. 4, top figs.). Both wet weight

Table 1.
A list of macrobenthic plants and animals in the *Mytilus* patch.

Sessile organisms		The other small animals	
Species	Presence/absence on *Mytilus* shell	Species	Life style
PORIFERA		PLATYHELMINTHES	
Halichondria sp. 1	+	*Notoplana humilis*	FL
Halichondria sp. 2	+	NEMERTINEA	
CNIDARIA		*Emplectonema gracile*	FL
Unidentified hydroid sp.	+	ANNELIDA	
TENTACULATA		*Lepidonotus* sp.	FL
Alcyonidium sp.	+	*Harmothoe imbricata*	FL
MOLLUSCA		*Genetyllis castanea*	FL
Mytilus edulis	+	*Nereis pelagica*	FL
Hiatella flaccida	−	*Nereis* sp.	FL
Musculus laevigatus	−	*Cirratulus cirratus*	TB
Modiolus modiolus difficilis	−	*Cirriformia tentaculata*	TB
ANNELIDA		*Terebellides stroemii*	TB
Hydroides ezoensis	−	ARTHROPODA	
Hydroides. elegans	−	*Lecythorhynchus hilgendorfi*	FL
ARTHROPODA		*Achelia* sp.	FL
Semibalanus cariosus	+	*Dynoides dentisinus*	FL
PROCHORDATA		*Cymodoce japonica*	FL
Styela clava	−	*Cleantiella isopus*	FL
Styela sp.	−	*Cleantiella* sp.	FL
Botryllus sp.	+	*Janiropsis* sp.	FL
CHLOROPHYTA		*Caprella mutica*	FL
Cladophora sp.	+	*Caprella* sp.	FL
Enteromorpha sp.	−	*Hyale barbicornis*	FL
Ulva sp.	−	*Hyale* sp.	FL
PHAEOPHYTA		*Atylus* sp.	FL
Ectocarpus sp. 1	+	*Amphithoe* sp.	TB
Ectocarpus sp. 2	+	*Jassa falcata*	TB

Presence (+)/absence (−) of sessile species on *Mytilus* shell and life styles of the other small animals are shown. FL, free-living species; TB, tube-building species.

and number of sessile species per unit surface area of *Mytilus* shell were also larger in the large mussels than in the small ones (Fig. 4, bottom figs.). A wet weight of 98% and an occurrence of 94% were observed on the large mussels. Of nineteen sessile species found in the patch, ten were observed on *Mytilus* shells (Table 1). All of these species except *Halichondria* sp. 1 and *Alcyonidium* sp. were only found on the large mussels. It was frequently observed that the sponges partly covered the other sessile species except for a bryozoan. However, no species were observed on the sponges. The juveniles of *Mytilus* attached to *Semibalanus cariosus* and the algae. Among the byssal threads, many tubes of *Hydroides* spp. were observed. *Hiatella flaccida*, *Musculus laevigatus*, and *Modiolus modiolus difficilis* were also seen among the byssal threads.

The large mussels with *Halichondria* sp. 1 had a high density of adhesive discs

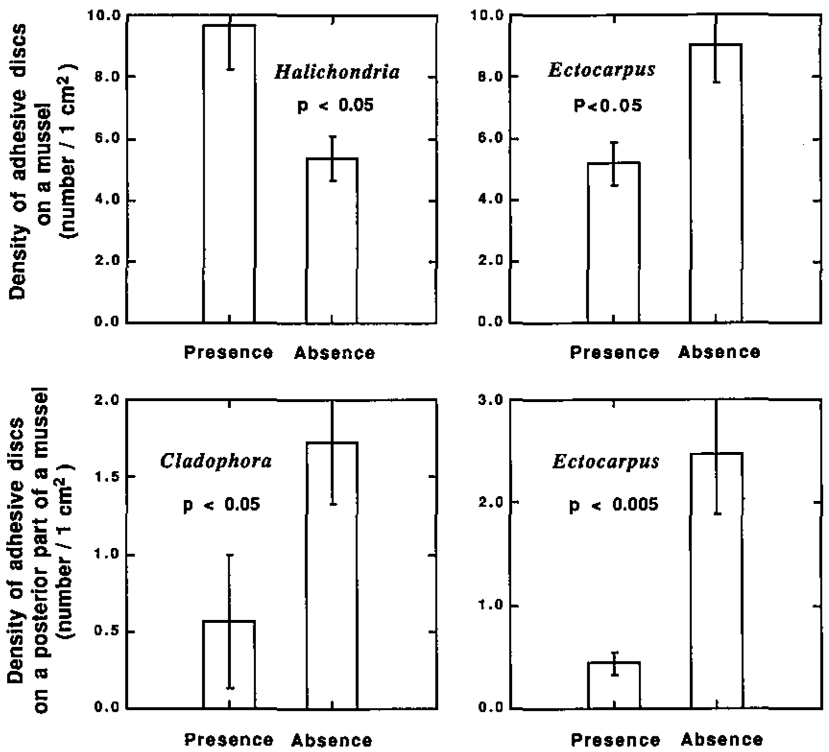

Fig. 5. Mean densities of adhesive discs on the large mussel shells (shell length ≧4.0 cm) with (presence) and without (absence) sessile species (a sponge and algae). Mean density for a mussel (top figs.) and mean density for a posterior part of a mussel (bottom ones). Vertical bars show ±1 SE. The 'large' mussels were divided into two groups by the presence/absence of sessile species. The Mann-Whitney U test indicates the significant differences between means for a sponge *Halichondria* sp. 1, for an alga *Ectocarpus* sp. 1, and for another alga *Cladophora* sp.

on their shells (U test, $p<0.05$; Fig. 5). On the other hand, those with *Ectocarpus* sp. 1 exhibited a low density of adhesive discs (U test, $p<0.05$). In particular, the density of adhesive discs on the posterior part of the shells was significantly lower in mussels with *Ectocarpus* than those without the alga (U test, $p<0.005$). Likewise, the density was also lower in mussels with *Cladophora* sp. than in those without the alga (U test, $p<0.05$). The shell length distributions were not significantly different for the 'presence' and 'absence' groups of large mussels for all sessile species (U test, $p>0.05$).

Discussion

The mussels in the patch which developed for 1 year were divided into two groups according to their shell lengths (Fig. 1). Hirano (1983) demonstrated that in Aomori Bay, the settling season of *Mytilus edulis galloprovincialis* (this mussel is probably the same species referred to as *M. edulis* in this study) lasted from October to July with a peak during April to June. The bimodal distribution of the mussel size seems to reflect settlements during the latter half of settlement peak in 1991 and during the first half in 1992. The maximum length of the mussel reached 7.0 cm, and this value was greater than that found in the rocky intertidal areas of northern Japan (Hoshiai, 1960 ; Tsuchiya, 1979 ; Tsuchiya and Nishihira, 1985, 1986 ; see also Suchanek, 1985). It suggests that the growth of *Mytilus* is more rapid in a sublittoral zone than in a littoral zone.

The shell morphology was different for the two size groups ; that is, the ratios of shell height and the ADM length to the shell length (i.e., slopes of regression lines shown in Fig. 2) were lower in the large mussels than in the small ones. In addition, it was found that the angles between the ventral margin and ADM of shells were not different for the two groups. Therefore, it was considered that the growth pattern of the mussel shell changed with size in this patch : the growth along an antero-posterior axis was more conspicuous in large mussels than in the small ones. Since there are inhalent and exhalent siphons at the posterior end of the mussel, this morphological characteristic of large *Mytilus* may be related to such biological activities as feeding and respiration. Although the number of adhesive discs was larger in the large mussels than in the small ones, the density on the posterior parts of mussels was lower in the large mussels. This indicates that the posterior part of the large shell was relatively freer from attachment of the neighbors than the small one, and occupied the peripheral part of the patch. On the other hand, since 80-85% of the adhesive discs were observed on the anterior parts of shells, the inner part of the patch was characterized by a high density of the byssal threads.

Ten species of sessile organisms were found on *Mytilus* shells (Table 1), but other species were not. Of the latter species, *Hiatella flaccida*, *Musculus laevigatus*, and *Modiolus modiolus difficilis* (all individuals were small ; shell length <0.9 cm) attached to the byssal threads of *Mytilus*. For these mussels, the byssal threads probably provide preferable settlement places. The sessile species found on shells were mostly observed in the large mussels. The wet weight and number of species per unit shell surface area were also higher in the larger mussls (Fig. 4). The algae, *Cladophora* sp. and *Ectocarpus* spp., were found in only the large mussel group; however, the shell length was not different for the groups of large mussels with and without algae. The densities of adhesive discs on the posterior part of large mussels were lower in mussels with *Cladophora* sp. and *Ectocarpus* sp. 1 (Fig. 5). Therefore, the peripheral part of the patch, which was occupied by the posterior parts of large shells, was an important habitat for the algal species. On the other hand, the large mussels with a sponge *Halichondria* sp. 1 had more adhesive discs than those without the sponge. For this sponge, the large mussels with many byssal threads, which probably occupy the inner part of the patch, may provide a preferable habitat.

These distribution patterns of sessile species on the mussel shell may increase the habitat heterogeneity of the *Mytilus* patch. Algae growing on the mussels at the peripheral part of the patch may provide microhabitats for epiphytic animals such as *Jassa falcata* and *Caprella* spp. Moreover, the algae may be important as a substrate for settlement of *Mytilus* larvae (e.g., Bayne, 1964). On the other hand, the effects of *Halichondria* spp. on the community in the *Mytilus* patch are worth investigating but remain unknown. It is also important to clarify the roles of semi-sessile (tube-building) species such as *Cirratulus cirratus* and *Terebellides stroemii*. On the surfaces of tubes, small animals such as foraminiferids and juveniles of mussels were observed.

The sponges often covered the other sessile species, and might be the best competitor for the mussel shell surface. Because the competition among sessile species for primary space is a determinant for their community structure, it is also important to evaluate effects of species interactions on the composition of sessile organisms which inhabit the *Mytilus* shell surface.

On the suspended rope, the spherical mass of *Mytilus* was formed in a short period by the settlement and the rapid growth of *Mytilus*. The sessile species inhabited the *Mytilus*, and diversified the physical stucture of the patch. In addition, colonizations by small animals such as polychaetes and amphipods usually occur rapidly in marine systems (Daen, 1981; Bros, 1987; Holmlund *et al*., 1990; Edgar, 1991, 1992). Therefore, the *Mytilus* patch established on the suspended rope, which is easy to manipulate, is a good study tool for habitat-community relationships. It is important to clarify the relationships between the habitat heterogeneity and the patch size/age for understanding the role of the habitat structure in community organization. In the intertidal area of this study site, Tsuchiya and Nishihira (1985, 1986) examined the effects of size and age of the *Mytilus* patch on the associated community, and indicated that the increase in environmental heterogeneity with the patch size and age increased the species

richness and diversity. The present study described characteristics of a habitat provided by *Mytilus*; the results strongly suggest that the 'live-in' patterns of sessile species on mussel shells are important, as well as the *Mytilus* population structure, for evaluating the habitat heterogeneity and for linking the habitat heterogeneity and the patch size and age. In contrast, the components of the community in this study were different from those observed on the intertidal rocky substrate (Table 1; see Tsuchiya and Nishihira, 1985, 1986); they included such subtidal species as *Styela* spp. and *Semibalanus cariosus*, but lacked the intertidal *Septifer* (*Mytilisepta*) *virgatus* and *Chthamalus challengeri*. The community also lacked limpets and decapod crustaceans. There characteristics in species composition may affect the community organization in the *Mytilus* patch established on the suspended rope habiat.

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